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VARIABILITY OF COURTSHIP OF THE BUCKEYE BUTTERFLY, *PRECIS COENIA* (NYMPHALIDAE)

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COURTSHIP BEHAVIOR OF BUTTERFLIES ranges from extremely stereotyped response in some species, to variability in other species (Scott, 1973). I have found that *P. coenia* has perhaps the most variable courtship of any butterfly studied to date. Mating of *P. coenia* was studied at Point Richmond, Contra Costa County, California, in connection with mark-recapture experiments (Scott, 1975), mainly by observing natural courtships and by releasing females in front of resting males.

Mate-locating behavior. *P. coenia* is a perching species as defined by Scott (1974a). Males perch primarily on bare spots of ground on fairly flat areas such as roadcuts and trails on hillsides, valley bottoms, and vacant fields. The larval foodplant (*Plantago lanceolata*) is most common in such sites, and females are most common near the foodplant. Males perch all day, especially from 0800 to 1400 (24-hour standard time). After 1400 fewer males show perching behavior, but some individuals still perch until 1600. Courtship and mating occur at the same time as male perching. 112 courtships and 27 copulating pairs occurred from 0815 to 1540, especially during the warmest part of the day. Virgin females were found at all times of day, and adults emerge from pupae in morning, indicating that some females wait until the day after emergence to mate. Females mate predominantly at the larval feeding sites, where males usually perch.

On cloudy or cold days few males perch and few courtships occur, but at temperatures of about 14-18°C individuals are able to perform most activities by basking (spreading the wings, moving the forewings forward, and orienting with the wings nearly perpendicular to the sun). Heinrich (1973) shows that

basking raises body temperature, and Blest (1975) showed that it may also reduce predation by displaying the eyespots which can startle predators.

Perching males sit on the ground and wait for a passing object. When an object appears, the male approaches near. Males investigate objects of a very wide size range. Three individual males followed for as long as possible investigated the following objects over a combined time span of two hours: a car (1 investigation); motorcycle (1); birds (11); a black and yellow butterfly (*Papilio zelicaon* Lucas) with 5 cm wingspan (2); an orange butterfly (*Colias eurytheme* Boisduval) with 4 cm wingspan (1); white butterfly (*Pieris rapae* L.) with 3 cm wingspan (2); other *Precis coenia* (32); a brown 2 cm wingspan butterfly (*Phyciodes campestris* Behr) (2); a white 2 cm wingspan butterfly (*Coenonympha tullia* Muller) (29); small grasshopper (1); small moths (2); small dragonflies (3); small bees and wasps (7); flies (5). These males sometimes investigated movement of vegetation due to wind, and made other investigative flights toward objects which I did not observe.

If the passing object is not another male or female *P. coenia* (of different appearance), the male usually returns to or near the previous spot. If a male chases another male which is flying past, the other male usually flies away when the perching male gets within 10 cm, and the perching male returns to the vicinity of his starting point. If two males which perch near each other investigate each other, they may separate or both may rise high in the air near each other then separate and descend to near the starting points, unless the encounter carries them too far away. Objects flying slowly (such as teneral males) seem to be pursued farther than erratically flying or swift objects, apparently because of greater resemblance to females. If a female passes by, the male pursues her for several meters until she lands, and courtship begins. Occasionally movement alone may be sufficient to attract the male for mating; one deformed female which could only hop erratically on the ground was found to be mated. Some females, especially older ones, are not pursued at all. If two males chase laterally more than ten meters from their previous sites, they seldom return. The males that were watched for up to several hours gradually moved over roughly a 30x30 m area, until they disappeared, usually because they pursued a female or another object for 20 m or more and did not return.

Courtship. Three stereotyped male and one female behavior patterns can occur in successful courtship: 1) *male hovering* consists of the male hovering in air by beating his wings at small amplitude, usually downwind just above the female; 2) *male fluttering* appears similar to male hovering but the male is on the ground behind the female, and the wings are usually moved with greater amplitude and lower frequency; 3) *male nudging* consists of the male, with his wings slightly raised and antennae pointing backward, pushing his head underneath the hind wings of the female (which are usually spread also) until his head is near her abdomen; 4) *female flapping* consists of the female on the ground flapping her wings at wide amplitude, continuously or in bursts (females flick their wings only occasionally when crawling during other activities).

Table 1 shows the association of these behavioral elements. In the simplest form of courtship, the female lands, raises her wings, the male lands behind, he moves alongside and bends his abdomen laterally (either right or left) to copulate. In a complicated courtship, after landing the female kept her wings spread, the male hovered then landed, the female flapped her wings and the male fluttered his, the male moved forward and nudged her, she raised her wings, he moved beside her and bent his abdomen to copulate.

Temporal patterns during courtship. Male hovering is most frequently observed just after the female lands either for the first time or after her short flights during courtship. The male then lands, whereupon male fluttering may occur. Male nudging generally occurs just prior to joining. Female flapping may occur whenever the male is on the ground just behind her. Virgins which are not very receptive often crawl or fly a short distance after being nudged. During courtship the female and male are sometimes quiescent, and movement by the female often leads to male nudging and abdominal bending.

Function of behavioral elements. Three behavioral responses during courtship seem to function similarly to the same responses in courtship of another Nymphaline butterfly, *Poladryas minuta* (Scott, 1974b). *Male hovering* and *male fluttering* are somewhat ritualized, but apparently help induce moderately unreceptive females to mate. *Male nudging* seems to function often merely as a technique for creeping under her wings if they are spread to enable the male to join; it may occasionally stimulate her to raise her wings to facilitate joining, and may also stimu-

late her to lower her abdomen so that joining may occur. Receptive females often raise their wings vertically and unreceptive females usually keep their wings spread. In one case the male nudged the female while her wings were raised. If the female does not lower her abdomen to slightly below horizontal or if she raises it slightly above horizontal, the male cannot grasp her. *Female flapping* is the "rejection dance" used to deter males. The females in Table 1 which copulated usually did not flap their wings or fly, but if they did, they flapped or flew weakly for a short time. Unreceptive virgin females flapped or flew less than did unreceptive mated females. When already mated females are pursued by males, the female generally flaps her wings vigorously upon landing, which seems to inhibit male responses somewhat (Table 1); then he usually flies away. The male may hover over the female for a moment. Female flapping resembles male fluttering closely, so may possibly cause the male to leave by convincing him that he is courting another male. Further evidence of this includes several observations in which a male chased another male, both landed on the ground and fluttered, then both flew away, and observations of general males flapping their wings when courted by another male. Females have other rejection behavior: 1) rarely an unreceptive female eluded a male by flying erratically. 2) an unreceptive virgin or newly mated female crawls or flies when the male tries to nudge or join; 3) she may raise her abdomen slightly so that he cannot copulate; 4) she keeps her wings spread, so that the male cannot crawl alongside to join and he must resort to "nudging." Courtship usually terminates unsuccessfully when the male departs. Sometimes, when hovering or crawling behind the female, he gets too far away and cannot relocate the female.

Role of vision and odor in courtship. Movement is necessary to elicit an investigative response by the male. By coloring all or part of a female's wings, I found that the general but not the detailed color pattern of the female is important in courtship. Virgin females with the upperside made completely black or red were usually ignored by males after a brief investigation, even though these females were courted for several minutes by other males before the females were colored. Females with several ocelli, white areas, or wings altered mated readily, however: one with the white areas on the forewings made black; one with the hindwing ocelli made green; one with the

ocelli of the left wings torn off. One female with crippled wings, and another less than half the normal size, had both mated. Males which had the dorsal wing surfaces blackened moved and apparently courted females normally (no copulations resulted because the females had already mated). One would expect the color and pattern of the male to be relatively unimportant because the male is behind the female during courtship.

The female might possess a pheromone. The shortest successful courtships involve nearly motionless females, which may indicate use of a pheromone for recognition. The most interesting observations concern interactions in which two males courted the same female; in three instances after one male joined, the other male continued attempts to join with the female, but did not attempt to join with the male of identical appearance. These males might have been able to recognize the female by following her movements during the interaction, or they might have used olfactory cues given off by one or both sexes.

Behavior during and after copulation. Immediately after joining, the male turns and faces opposite the female. Copulation lasts an average of 27 minutes (14-59, $S = 11.5$, $N = 14$). The female is more active than the male during copulation; she usually spreads her wings to bask, but the males does so only in about 30% of the copulating pairs. When disturbed, it is the female which carries the dangling male in flight; of 12 copulating pairs that were stimulated to fly, females flew 22 times, males never flew (some copulating pairs flew more than once). Copulation ends by the female crawling away dragging the male, and the female kicks with the hind legs and may turn until the male is broken off. The male then flies and the female remains for a short time.

Duration of courtship. Successful courtship lasted from only ten seconds when all wing movements and male nudging were eliminated, to 10 minutes 20 seconds. Unsuccessful courtship with virgin females lasted from 30 seconds to 20 minutes (often), rarely up to 9 minutes. Courtships with unreceptive mated females almost always lasted less than a minute.

Number of matings. Males probably can mate many times since they perch and mate at all ages, but only one male is known to have mated twice. Number of female matings was determined by counting spermatophores. Females predominant-

ly mate once, but occasionally mate twice and rarely three times (Table 2).

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Table 1.—Association of some of the behavioral elements of courtship: successful courtship of virgin females (left of the three positions separated by two dashes); unsuccessful courtship of virgin (middle) and mated (right) females. Terms are defined in text. Flying refers to a female flying during courtship.

Male	Female				Totals
	flapping, flying	flapping	flying	neither	
hover, flutter, nudge	-2-	-2-	- -	- -	-4-
hover, flutter	- -1	-2-	-1-	- -1	-3-2
hover, nudge	-3-1	1-2-1	-1-	1-1-	2-7-2
flutter, nudge	- -	2-1-1	-1-	-1-	2-3-1
hover	-3-3	1-5-3	-2-1	-5-	1-15-7
flutter	- -	-1-2	2-1-	2-1-	4-3-2
nudge	- -1	-4-1	- -	1- -	1-4-2
neither	-1-	1-3-15	1- -1	2- -	4-4-16
Totals	-9-6	5-20-23	3-6-2	6-8-1	14-43-32

Table 2.—Relationship between number of matings and apparent age (wing condition) of wild caught females. Totals are larger than sum of females rated once or twice because some females were not graded for wing condition.

	0	Wing Condition				Total	
		Young	Old				
	38	0	0	0	0	38	
Number of	1	23	9	12	11	7	95
Spermatophores	2	1	2	5	5	3	17
	3	0	0	0	0	1	1